MOVEMENT AND TERRITORIALITY OF WINTERING HERMIT THRUSHES IN SOUTHEASTERN LOUISIANA

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ABSTRACT.—We describe the spatial organization and social behavior of Hermit Thrushes (*Catharus guttatus*) wintering in pine plantations and an adjacent hardwood forest in Tangipahoa Parish, Louisiana over three winters. We used point counts (n = 403) to collect data on agonistic behaviors and relative abundance within the study area. We used mist-netting to study site fidelity on four 9-ha plots within and among years. We used radio-telemetry to measure Hermit Thrushes' movements and territoriality (n = 50). We found that Hermit Thrushes saturated suitable patches within the study area. Most Hermit Thrushes actively defended small [mean = 0.55 ± 0.03 (SE) ha], minimally overlapping (15.90 ± 3.63%) territories throughout the winter. Hermit Thrushes established and maintained territories using the same agonistic behaviors described for breeding birds. A few non-territorial birds (14%) moved among occupied territories, but most were faithful to a larger neighborhood, apparently awaiting a territory vacancy. Territorial behavior and frequency of non-territorial birds did not differ among age and sex classes, suggesting the absence of a sex- or age-based dominance hierarchy. The behavior of Hermit Thrushes conformed to the emerging view that competition for spatially mediated resources on the wintering grounds, such as food or cover, contribute to limiting populations of many species of migrant passerines. *Received 10 Dec. 1999, accepted 11 May 2000.*

The winter behavioral ecology of most species of migratory landbirds is poorly understood. In general, we know that migrant passerines employ a variety of behavioral strategies during the winter to deal with specific environmental conditions (Rappole and Warner 1980, Hagan and Johnston 1992). The species specific behaviors used to deal with spatial limitations have important implications for models of population regulation and the development of conservation strategies (Sherry and Holmes 1996).

Local winter spatial strategies are highly variable among species of migrant songbirds. The absence of breeding activities frees many species to move with the protection of a flock or to live solitary, vagrant lifestyles. Many species, including perhaps a majority of non-flocking migrant passerine species, establish resource-based territories that are defended for at least part of the wintering season (Rappole and Warner 1980, Holmes et al. 1989, Winker et al. 1990). Territory defense and exclusion based only on resource availability are likely indicators that habitat availability and food resources are limiting factors during the winter (Brown 1969). Before questions about habitat and food resource use can be answered, it is necessary to describe the basic winter behavioral ecology of a population or species. Several detailed investigations of territorial wintering migrants have revealed that dominant individuals are able to maintain stable territories throughout the winter, while some subordinate birds are forced into a non-territorial strategy in search of resources (Rappole et al. 1989, Winker et al. 1990, Marra et al. 1993, Wunderle 1995). Floater (non-territorial) behaviors have only recently been recognized within wintering populations (Smith 1978, Winker et al. 1990, Stutchbury 1991), although the behavior may be as common as on the breeding grounds.

Floaters are also considered indicators of habitat and/or food resource limitation, providing important insight into a population's local distribution (Brown 1969). The potentially diverse behavioral patterns of floaters make them difficult to categorize and sometimes difficult to detect.

Among forest thrushes, only Wood Thrushes (*Hylocichla mustelina*) and Bicknell's Thrushes (*Catharus bicknelli*) have been studied on their wintering grounds. Many Wood Thrushes that wintered in Veracruz, Mexico had stable territories, but a large subset of the population exhibited a wandering strategy of spatial use (Rappole et al. 1989, Winker et al. 1990). Similarly Bicknell's Thrushes are territorial on their wintering grounds and some may be floaters (McFarland and Rimmer, pers. comm.). Gram and Faaborg (1997) reported

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that wintering Hermit Thrushes in Mexico also might be territorial.

We investigated patterns of spatial use and social behavior by short-distance migrant Hermit Thrushes (*Catharus guttatus*) wintering in southeastern Louisiana. We hypothesized that intraspecific competition results in a behaviorally mediated system of territoriality. This hypothesis leads to three questions. Does the winter behavior of Hermit Thrushes conform to the standard definitions of territoriality? Do alternative classes of behavior exist within the system of territoriality (i.e., floaters)? Finally, does a dominance hierarchy among sex and age classes affect Hermit Thrushes' spatial distribution?

METHODS

The study area, located in northern Tangipahoa Parish, Louisiana (30° 41′ N, 90 28′ W), is a 30 km² loblolly pine (*Pinus taeda*) plantation isolated by a mixed landscape of riverine hardwood forest, agricultural land, and rural housing. The pine plantation is a mosaic of even-aged stands ranging in size from 2 to 244 ha [mean = 53.84 ± 9.59 (SE) ha] and represents a continuum of age classes from clearcut to mature forests (20–30 years).

We conducted point counts for three winters (1996–1997, 1997–1998, 1998–1999) during five distinct periods: arrival (15–31 October), fall (1–30 November), early winter (1 December–31 January), late winter (1 February–14 March), and spring (15 March–30 April). We located all point counts within the study area but outside of mist-netted plots. Point count locations were seperated by at least 120 m. Three observers conducted 422 point counts at 191 locations.

We used point counts ($n = 120$) conducted during the arrival and fall periods to study arrival time, relative abundance, and intensity of vocalizations in the study area. Arrival and fall point counts were conducted as 10 min silent surveys without any playback solicitation. We repeated 40 replicate point counts twice during the arrival period and once during the fall period at ten day intervals.

We used winter and spring point counts ($n = 283$) to quantify relative abundance and agonistic behaviors. Winter and spring point counts always began with a 10 min quiet period, followed by 5 min of playback recordings of Hermit Thrush songs and calls. For all point counts, we counted Hermit Thrushes and recorded the time, distance, and method by which each Hermit Thrush was originally detected, and the occurrence of agonistic displays. We tested for changes in the level of vocalizations through fall and winter using contingency table analysis of detections with and without playback.

We used four 9-ha study plots, each with 28 mistnets arranged in a grid, to study the movements, site

fidelity, and over-winter persistence of individual birds. We passively netted each plot for 2 days (one period) every 5–6 weeks from November to April for all three winters. In addition, once each year in early winter and again in late winter we used playback recordings and a decoy in an attempt to capture and resight every bird on the plots (Sliwa and Sherry 1992, Graves 1996). All captured birds were color banded and aged as either hatch-year/second-year (HY/SY) or after-hatch year/after-second year (AHY/ASY) based on criteria of Pyle (1997). Dwyer (1998) used a molecular technique to sex many of the Hermit Thrushes captured during the winters of 1996–1997 and 1997–1998. We obtained few behavioral observations of known age ($n = 58$) and known sex ($n = 11$) birds because only captured birds could be aged and sexed.

We used radio-telemetry of birds netted on study plots to determine if individuals exhibited territorial or floating patterns of movement, as well as to quantify territory size, rates and distances of movement, and interactions with neighbors. We put radio transmitters on 50 Hermit Thrushes captured on the four study plots with transmitters weighing 1.8 grams (Wildlife Materials Inc.), attached to a trimmed interscapular feather tract with epoxy glue.

A single observer triangulated bird locations, usually with at least three bearings, and separated consecutive locations by at least 45 min to insure independence (Swihart and Slade 1985, White and Garrot 1990). We estimated locations to be accurate to within 5 m at a distance of 100 m based on triangulation to transmitters at known locations. We plotted locations by hand, and used RANGES V for spatial analysis of territory size, distance moved between locations, and interaction between neighboring individuals (Kenward and Hodder 1996). We estimated territory size with the minimum convex polygon (MCP) method after visual comparisons with more robust harmonic mean and Kernel methods showed that MCPs estimated biologically meaningful home ranges with fewer location samples. We used incremental analysis, which plots changes in territory size as sample size increases, to determine the minimum number of locations necessary for a good MCP estimate of territory size. We identified floaters by visual inspection of the distribution of MCP size among individuals. We measured movement rate of individuals as the straight-line distance between consecutive locations.

Amount of territory overlap provides information on level of saturation and potential for interaction between neighbors. Measuring territory overlap requires simultaneously radio-tracked groups of individuals and biologically meaningful estimates of territory boundaries. We used harmonic mean estimates of territory boundaries to compute overlap because they visually reflected the areas used most intensely by radio-tagged birds better than MCP or Kernel methods. Harmonic mean home range estimates are extremely biased to grid cell spacing (White and Garrot 1990). We used the program TRACKER (Angerbjorn 1994) instead of RANGES V for this analysis because it suggests a grid

cell spacing based on the density of locations. Because harmonic mean estimates of home range are more robust when built from large sample sizes, we limited the analysis of territory overlap to birds with at least 30 locations.

Dynamic interaction is a measure of the attraction, repulsion, or indifference between neighboring individuals. It uses temporally coinciding locations to compute the distance between actual locations of an individual and randomly selected potential locations of its neighbor. Because there was some overlap in the neighborhood of nine simultaneously tracked birds, we conducted a dynamic interaction analysis to determine if pairs of birds were actively avoiding each other. Dynamic interaction analysis is based on Jacob's Index; calculated with Ranges V; Kenward and Hodder 1996). Jacob's values approaching 1.0 indicate that simultaneous locations of a pair are closer to each other than the distance between their territory centers given equal likelihood that they could be anywhere on their territory at that time. Values approaching −1.0 indicate birds are farther away from each other than by chance alone. We used SYSTAT 8.0 for all non-spatial statistical analysis, statistics are reported as mean ± SE.

RESULTS

Fall point count surveys showed that Hermit Thrushes began to arrive on their wintering grounds in southeastern Louisiana during the second week of October. Density and abundance increased rapidly and stabilized by the end of the third week in October. Territorial vocalizations as measured by point count detections without playback increased with population density and peaked in the fall before declining early in winter (Fig. 1). Density, as measured by number of detections with playback, remained high through the early winter period, although the frequency of vocalizations declined as indicated by fewer birds detected during the silent period of point counts (χ^2 = 109.83, n = 260, P < 0.001).

We detected 263 Hermit Thrushes at 283 winter points counts with at least one detection at 52% of locations. Only 11% of the Hermit Thrushes we detected at winter point counts were detected before the playback of vocalizations.

Wintering Hermit Thrushes displayed a variety of agonistic behaviors, most of which are commonly used on the breeding grounds (Dilger 1956, Jones and Donavon 1996). At winter point counts with playback, 82% of Hermit Thrushes were first detected by *chup* notes. Only 2% were first detected visually. Almost all non-playback detections were by *chup*

FIG. 1. Point count detections of Hermit Thrushes in southeastern Louisiana with and without playback of Hermit Thrush vocalizations. Detections without playback are dependent on vocalizations by Hermit Thrushes, while total detections with and without playback more accurately reflect actual density. Arrival = 15–31 Oct., fall = 1–30 Nov., early winter = 1 Dec.–31 Jan., late winter = 1 Feb.–14 Mar., spring = 15 Mar.–30 Apr.

notes. Other detections were made by a high pitched *wheez* note (10%), a catbird-like *rank* vocalization (3%), and wing winnows (1%; see description of behaviors in Jones and Donovan 1996). We heard singing in the form of soft, whispering song several times both with and without playback, usually soon after fall migration. Common agonistic visual displays included tail- and wing-flicking, crest raising, foot quivering, bill snapping, puffing, and stretching. We recorded agonistic displays during almost every visual observation that followed playback recording of Hermit Thrush vocalizations.

Intraspecific agonistic interactions between two or more Hermit Thrushes, such as chasing or perch displacement, were observed in about 21% of playback events. We recorded behaviors of 11 individuals of known sex and 58 individuals of known age. Females (n = 9) and males (n = 2) displayed most of the common aggressive behaviors. Similarly, all behaviors were observed in both HY/SY (n = 43) and AHY/ASY (n = 15) age groups.

We captured 206 individual (newly banded) Hermit Thrushes in 24,416 hours of passive mist-netting. Thirty-seven percent of all captured individuals were AHY/ASY and 74% of 82 sexed individuals were female (Dwyer 1998). Capture rate of Hermit Thrushes in-

cluding recaptures (within the same year), returns (between years), repeats (same day or period), and unbanded birds was 1.4 per 100 net-h. We captured 65 additional individuals and 24 recaptures using playback and decoys, for a total of 271 individuals captured. We recaptured 95 (35%) of these within a year (but different period). Twenty-five (18% of individuals banded in the first and second years) returned in subsequent years to winter on the same study plot. The age ratio of returning individuals in their first year of capture did not differ from the age ratio of all individuals captured ($\chi^2 = 0.21$, $n = 323$, $P > 0.05$). Similarly, the sex ratio of returning Hermit Thrushes (75% of 12 were female) did not differ from the overall ratio in the study area (Fisher Exact Test: $\chi^2 = 0.03$, $n = 94$, $P > 0.05$). Of the 25 returns only two were captured more than 30 m from the net where they were originally captured. We never captured or observed any marked Hermit Thrush at more than one 9 ha plot or at more than one point count location.

We radio-tracked 50 Hermit Thrushes. Radios fell off after an average of 21.76 days (± 1.98, range = 2–53). During the period when radios were attached, we collected an average of 26.44 ($\pm$ 2.5, range = 3–63) locations per bird. Incremental analysis of 12 home ranges showed that MCPs begin to plateau after 10–20 locations. Seven radio equipped Hermit Thrushes were categorized as non-territorial based on their large home range sizes. Of the remaining birds, we had enough locations (>10) to make territory size comparisons for 34 Hermit Thrushes. Nine birds with transmitters were not included in the analysis because of small location sample sizes. Territory sizes averaged 0.55 ± 0.03 ha, (range = 0.22–0.97 ha). Territory sizes did not differ between sexes ($F_{1,14} = 0.164$, $P > 0.05$), or between age groups ($F_{1,32} = 1.212$, $P > 0.05$). We located nine birds at night, all roosting within their territories.

Most Hermit Thrushes (85%) maintained territories with a MCP less than 1 ha. We classified seven birds with large MCPs as floaters (5.83 ± 1.06 ha, range = 2.53–11.3; Fig. 2). The average distance between consecutive locations for territorial birds was 55.30 ± 1.59 m. In contrast, floaters moved an average of 121.28 ± 25.36 m between locations, two
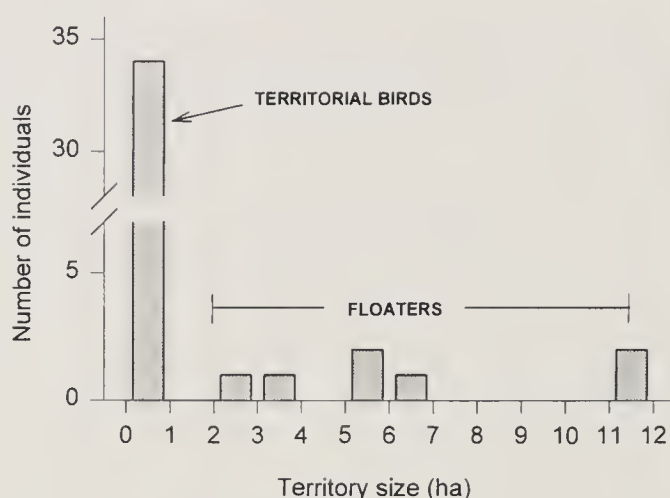

FIG. 2.   Minimim convex polygon territory size for 41 Hermit Thrushes. The large gap in the distribution between 34 individuals with territories smaller than 1 ha and 7 individuals with larger territories was used to characterize floaters.

floaters moved more than 1 km between locations (Fig. 3A). Floaters sometimes displayed aggressive behavior similar to that of territorial birds. One floater was originally captured using playback vocalizations and another responded to playback after its radio failed. Dwyer (1998) sexed two floaters; one was a male and one was female. Age of floaters (5 HY/SY, 2 AHY/ASY) did not differ from the age ratio of all other captured Hermit Thrushes (65% HY/SY).

Of nine simultaneously radio-tracked neighboring birds, eight had distinct, abutting territories. The analysis revealed little territory overlap except for one bird that we categorized as a floater. We simultaneously radio-tracked four additional pairs and one triad with overlapping or abutting home ranges. Overlap between territorial birds averaged 15.90% ± 3.63%, $n = 21$) and ranged from 0–79% of territory area (Fig. 3B). Every combination of overlapping pairs scored near zero on Jacob's Index, indicating that birds were indifferent to each other (mean = 0.005 ± 0.005).

DISCUSSION

Banding data indicated that many wintering Hermit Thrushes were site faithful from November to March. Ninety percent of within year recaptures occurred at the same net (45%) or a net within 80 m (the average diameter of a territory). Hermit Thrushes did not move out of their territories to roost elsewhere
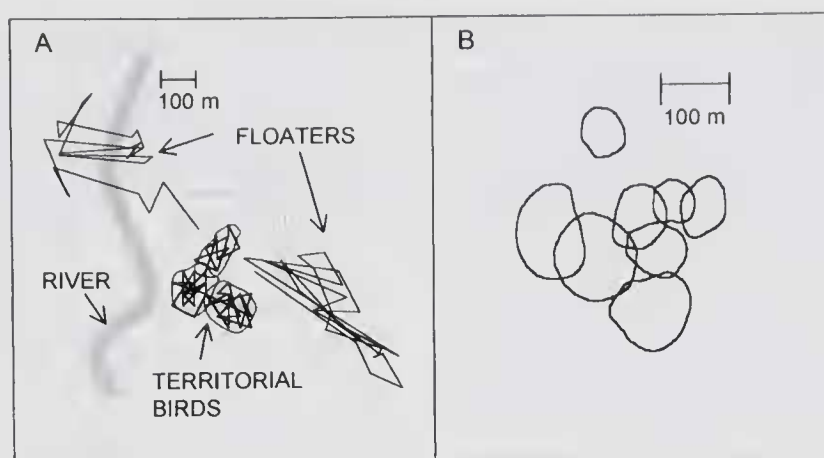
FIG. 3. Movements of Hermit Thrushes wearing radio telemetry transmitters. A. Movement patterns of two floating and three territorial Hermit Thrushes in relation to 9 ha mist-net plot (box). Home range contours are also shown for territorial birds. Lines indicate movements between successive locations. B. Territory contours (95% hamonic mean method) of eight simultaneously radio-tracked Hermit Thrushes showing variation in territory size and overlap among neighbors. A floater that moved among territories of these individuals is not shown.

at night. Although only 18% of Hermit Thrushes returned between winters, the individuals that returned used the same territory as in previous winters. Additional Hermit Thrushes may have returned to the area, but relocated outside of our plots. Telemetry data indicated that most wintering Hermit Thrushes maintained distinct, minimally overlapping territories. High vocalization rates during the initial settlement indicated aggressive territory establishment. The lack of spatial interaction between neighboring individuals and the low level of vocalizations following settlement suggests that once territory boundaries were established, boundary maintenance was minimal.

Hermit Thrushes that did not establish a stable territory in a suitable habitat were lumped into the broad category of floaters. The term floater has been used to describe two different patterns of behavior for non-breeding birds. First, floaters have been characterized as indiscriminate wanderers, perhaps faithful to particular habitats, but not defending specific territories. Usually such floaters are recognized only as individuals not recaptured or resighted in repeated mist-netting and spot-mapping periods (Bates 1992). The second explanation characterizes non-breeding season floaters as secretive but intent subordinates, stalking selected territories in search of vacancies (Smith 1978). In general, floaters are thought to be at a behavioral disadvantage to

territorial birds and experience lower survival relative to territory holders (Brown 1969).

Collectively, the floaters we monitored do not fit into either definition but showed a diverse array of spatial strategies. For instance, one radio-tagged bird had a very small core home range but otherwise wandered widely among neighboring territories and surrounding habitats. We suspect this bird may have been looking for a new, less constrained territory but was encountering spatial pressure wherever it wandered. Another individual crossed a 60 m wide river channel more than 10 times during 2 months, moving back and forth between two habitats. Two other Hermit Thrushes moved long distances (0.6 km and 1 km) before radio contact was lost. One pattern was consistent among all the floaters in this study: they chose alternatives to territoriality instead of establishing territories in unsuitable habitats (i.e., clearcuts).

We found no evidence that winter territorial behavior of Hermit Thrushes resulted in dominance of males over females or older over younger age groups, although we had small sample sizes for these comparisons. Females used agonistic calls and displays as did males, and females maintained territories of the same size as males. Males as well as females behaved as floaters, and females returned to the same territory between winters as frequently as males. Similarly, younger Hermit Thrushes used agonistic behaviors to successfully de-

fend territories that did not differ in size from those of older individuals. Finally, younger Hermit Thrushes were no more likely to be floaters and returned between winters at the same frequency as older Hermit Thrushes. Territorial wintering species with obvious morphological differences between age and sex classes, like American Redstarts (*Setophaga ruticilla*) and Hooded Warblers (*Wilsonia citrina*), quickly sort into distinct dominance hierarchies after arriving on their wintering grounds (Holmes et al. 1989, Stutchbury 1994). In contrast, the subtle morphological differences between age and sex classes of Hermit Thrushes may be related to our failure to detect a dominance hierarchy. The absence of dominance hierarchies during the winter might be expected in other monomorphic migrant species (Bates 1992).

We have provided four types of evidence that suggest Hermit Thrushes saturate suitable patches within the local landscape. First, Hermit Thrushes aggressively defended resources with agonistic vocalizations and displays that are also used on breeding grounds for territory defense. Second, Hermit Thrushes occupied distinct home ranges that abut or slightly overlap with neighboring conspecifics. Third, some individuals behaved as floaters, moving within and among territories of other individuals. Finally, vacated territories were quickly occupied by either expanding or shifting neighbors, or floaters. Two territories vacated by Sharp-shinned Hawk (*Accipiter striatus*) predation were reoccupied within one week by vocalizing Hermit Thrushes. We do not know if replacements were floaters or territorial neighbors that occupied the open space. In either case, rapid replacements indicate saturation.

Wintering Hermit Thrushes defended smaller territories at higher densities than eastern populations of breeding Hermit Thrushes. Martin (1960) estimated territories in Ontario, Canada averaged 0.72 ha. Jones and Donovan (1996) reported mean sizes of 2.5 ha (range = 0.5–14.3) from 12 breeding season studies. In comparison, we estimate 0.56 ha based on telemetry data from all plots. Our estimates of territory size are similar to those found for Wood Thrushes wintering in Veracruz, Mexico (Winker et al. 1990).

Winker and coworkers (1990) using telem-etry, estimated that 50% of the Wood Thrushes in Veracruz, Mexico were floaters, compared to 14% of Hermit Thrushes in our study. The higher proportion in Mexico might be caused by more pronounced habitat limitations than occur in southeastern Louisiana.

Site fidelity between winters is an important indicator of breeding season survivorship and winter habitat quality. The proportion of Hermit Thrushes returning between winters in our study is lower than for all other studied species of migratory passerines. Other researchers on wintering passerines report overwinter returns near 50% (Nisbet and Medway 1972, Price 1981, Winker et al. 1990). Differences may be due to species-specific survivorship and dispersal patterns. Other studies of wintering Hermit Thrushes report return rates similar to ours. In South Carolina, 13% of 81 birds returned between winters (Bent 1964), and in California, 18% of 306 returned between winters (reported in Jones and Donovan 1996). Estimates for Hermit Thrushes, including our own, might be biased low by sampling methods or species-specific behaviors. Long-term studies would allow for more robust mark-recapture analyses and increase the accuracy of these estimates.

The behaviors of wintering Hermit Thrushes in southeastern Louisiana clearly conform to Nice's definition of Type-E winter territories (Nice 1941). Territoriality in non-breeding migrants is now a widely recognized behavior, but its function in population regulation is not fully understood (Rappole and Warner 1980). The evidence for overlapping territories and the presence of a floater class confirms that the distribution of wintering Hermit Thrushes in southeastern Louisiana agrees with Brown's (1969) Critical Density Level 3. Most birds actively defend distinct, minimally overlapping territories, probably in response to some limiting resource (i.e., food or space).

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